"On some Thallophytes parasitic within recent Madreporaria." By P. Martin Duncan, M.B. Lond., President of the Geological Society, F.R.S., &c. Received March 17, 1876 *.

[Plates 5, 6, 7.]

Contents.

I. *A Notice of the Discoveries of previous Observers.*

During some investigations into the nature of the sclerenchyma of the Stony Corals (Madreporaria) I was impressed with the importance of examining the method of entry, growth, and distribution of the minute unicellular parasite which so constantly penetrates and ramifies in minute tubular excavations in the solid structures.

The interest of the subject struck Quekett in 1851; for he described the minute tubules of a parasite in his Lectures, which he subsequently published in 1854. He wrote as follows:—"Confervoid growths are also very frequently met with in the skeleton of corals, as all those bodies possess animal matter, which, decomposing after death, becomes a nidus for the development of Confervæ; and hardly a section can be examined without exhibiting such an appearance as shown in fig. 78"†. This figure exhibits almost straight canals, of great tenuity and of different lengths, cutting across the normal structures at different angles.

Before this time, Carpenter‡ and Bowerbank§ had shown that molluscous shells contained tubular structures; and Quekett, in his work, agreed with them as regards their facts; but he believed (as, indeed, Carpenter did also at that time) that, whilst some of the tubules

* Read May 11, 1876. See *antè*, p. 17.

† John Quekett, 'Lectures on Histology,' vol. ii. p. 153 (1854).

‡ Carpenter, in Todd's 'Cyclopædia of Anatomy and Physiology,' article "Shell," vol. iv. p. 562 (1852); Ann. & Mag. Nat. Hist. Dec. 1843; Report Brit. Assoc. 1844, 1847.

§ Bowerbank, Trans. Microsc. Soc. i. (1844).

were normal to the shells, others were the product of "Confervæ, Spongida, or of minute boring animals."

In 1851 Mr. C. B. Rose, F.G.S., found minute tubular borings in fossil and recent fish-scales; and he published his admirable and short researches in 1855, illustrating them with great care and truthfulness. He noticed that it required a magnifying-power of a $\frac{1}{4}$-inch-focus object-glass to trace the course of the tubes with any degree of distinctness; and he pointed out that their minute diameter of $\frac{1}{2000}$ to $\frac{1}{4000}$ inch distinguished them from the results of boring sponges. Mr. Rose did not attribute the tubes to Confervæ, but to the operation of "infusorial parasites"*.

In 1858, C. Wedl† contributed a paper on the subject of these canals in shells. He described and delineated them; and some of his drawings agree remarkably with those of Mr. Rose. He carried the examination of his specimens much further. He investigated the parasitic canals in recent shells and in fossil Gasteropoda, Bivalves, and Brachiopoda, discovering them even in a *Leptæna* from the Devonian formation. Moreover he exposed a recent shell to the action of dilute hydrochloric acid, and by dissolving the carbonate of lime exposed the vegetable organism. He considered that the parasite was *Saprolegnia ferax*, Kütz., which he termed a confervan. He did not examine any corals.

About the same time, Kölliker‡ contributed a paper to the Royal Society, which contained notices of his having seen the parasitic tubes in a great many shells, Sponges, Foraminifera, and recent Corals; but he did not advance further than C. Wedl in their description. He noticed, however, that the parasite was unicellular in its construction, and wrote:—"I may further add that the frequent anastomoses of the parasitic tubes remind one of the anastomoses observed in the mycelium of some unicellular fungi; whereas such connexions have not yet, so far as I know, been observed amongst the Confervæ." He stated that the sporangia were quite of the same kind as those of unicellular fungi, and that it seemed probable "that the parasites dissolve the carbonate of lime of the hard structures into which they penetrate, by means of exudation of carbonic acid, which secretion would seem to take place only at the growing ends of the fungial tubes, as they never lie in larger cavities, but are always closely surrounded by the calcareous mass." He considers it possible for the parasite to bore its canal by mechanical force in the horny fibres of sponges, in the way that similar parasites make their way through the cell-membranes of Confervæ and other plants.

Finally, this short history would be incomplete without the interesting notice by Mr. H. N. Moseley which was contributed to the Royal Society

* Rose, Quart. Journ. Microsc. Soc. 1855, no. x. p. 7, "On the Discovery of Parasitic Borings in Fossil Fish-scales" (read June 1854). (Plate in vol. iii. plate i.)

† Sitzungsb. d. k. Akad. d. Wiss., December 1858, Band xxxiii, no. 28.

‡ Proc. Roy. Soc. June 9th, 1859, vol. x.

after I had become engaged in these investigations. He writes*:—"*Vegetable Parasites.* The corallum of both *Millepora* and *Pocillopora* is permeated by fine ramified canals, formed by parasitic vegetable organisms of the same nature as those described by Dr. Carpenter and Prof. Kölliker as occurring in the shells of mollusks &c. The organisms were found in abundant fructification; they were *green*, but otherwise appear to be fungi, as are the parasites of shells &c. Similar parasites are to be found in various coralla from widely distant parts of the world."

The paper communicated by me to the Geological Society "On some Unicellular Algæ parasitic within Silurian and Tertiary Corals, with a Notice of their Presence in *Calceola sandalina* and other Fossils," was read Jan. 19, 1876 (Quart. Journ. Geol. Soc. vol. xxxii. p. 205).

II. *The Range of the Parasites, and a List of Species examined.*

Both Kölliker and Mr. Moseley have shown that corals from different localities and belonging to widely remote seas are affected by the parasitic organisms.

Having found the ramifying tubules and their contents in the corallum of *Flabellum laciniatum*, Edw. & H., from the neighbourhood of Davis Straits, at a depth of 380 fathoms, and in *Balanophyllia verrucaria*, Pallas, from the Mediterranean, at different but not great depths, the previously known range may be thus increased. All the deep-sea corals examined from the bed of the North Atlantic are more or less affected by the parasite, and the littoral forms also. Thus in *Caryophyllia clavus*, var. *borealis*, from a depth of 1 to 30 fathoms, in *Lophohelia prolifera*, from 422 fathoms, and in *Solenosmilia variabilis* (nobis), from 1095 fathoms, the tubes were found in greater or less abundance.

The specimens examined by Kölliker and Mr. Moseley were mostly from seas with a high temperature; and the species of coral to which reference will be made in this communication were located during their lifetime in temperatures from 39°·7 to 55° Fahr. The bathymetrical range of the unicellular parasite is therefore from low-water mark to 1095 fathoms in the northern seas; and the temperature to which it is subject varies from 39°·7 to that of the surface water. But it is evident that it is the most destructive when the pressure is least and the warmth of the sea is greatest; and therefore corals of genera such as *Caryophyllia* and *Balanophyllia*, which are grown in aquaria, exhibit the parasite in perfection.

The range of the coral-parasites in time, whilst admitting that there may be and may have been more than one species, is very great. They may be found in Upper-Silurian corals and in those of later date down to the Tertiary times; and tubular excavations corresponding in their appearance may be found in some calcareous fossils of the Lower

* Proc. Roy. Soc. Nov. 25, 1875, vol. xxiv. p. 64.

Silurian rocks*, filled more or less with the fossilized vegetable matters, the cell-wall being even preserved in the Tertiary forms.

List of Species of Corals examined.

†*Caryophyllia clavus*, Scacchi, var. *borealis* and var. *Smithi*. Range of specimens, low spring-tide to 90 fathoms.
†*Flabellum laciniatum*, Edw. & H. 380 fathoms.
†*Lophohelia prolifera*, Pallas. 90 to 422 fathoms.
‡*Solenosmilia variabilis*, Dunc. 1095 fathoms.
§*Balanophyllia verrucaria*, Pallas. Littoral.
‖*Millepora alcicornis*, Forsk. Littoral.

III. *Method of Investigation.*

The parasitic growths which occur in the dense sclerenchyma of the Madreporaria are best seen by examining thin transverse and longitudinal sections of recently dead corals, and also by submitting whole or parts of specimens to the action of very dilute hydrochloric acid and thus obtaining the remains of the organisms. The upper parts of the corals, which are covered with the soft tissues just before death, are comparatively free from the ravages of the destructive tube-matters; but the lower portions of the corallum (which have, especially in species with endotheca, been long uncovered by living tissue) are usually crowded with the borings of the parasites. Age and the length of time which has elapsed since the removal of the corals from the sea have no influence on the preservation of the canals bored within; for they may be traced in fossil specimens, and also in recent forms which have been half a century or more out of the sea. Moreover, so lasting is the peculiar organic basis on which the parasite depends and in and about which the granules and spicula of carbonate of lime are deposited during coral-growth, that it may be extracted more or less perfectly by weak acids from the oldest corallites which have not undergone fossilization; and in the instances of some mid-Tertiary reef-building forms I found it to be distinguishable. The most complete organic films are to be obtained from corals recently dead. The continued preservation of the vegetable cell-wall and its cytioplasm appears to depend upon the same causes which determine that of the organic film. Sometimes the delicate tubular cell-wall may be traced, in old specimens decalcified, amidst the organic matter; and I have noted its preservation in a Miocene coral ¶ as a transparent and probably mineralized structure; but usually age appears to affect the cell-wall, which is commonly found in a very indifferent condition and more or less imperfect in old and dry specimens. In some fossils the spores, either oospores or conidia, are found in a wonderful state of pre-

* P. M. Duncan, Proc. Geol. Soc. (abstract of communication) for Jan. 19, 1876.
† From the North Atlantic. ‡ From the Spanish coast.
§ From own aquarium. ‖ From Bermuda.
¶ Quart. Journ. Geol. Soc.

servation; their shape is perfect and they have been carbonized. Moreover, the cytioplasm, so transparent or minutely granular in most recent specimens, is to be recognized in old corals after they have been decalcified, and in fossil corals also, in the form of dark linear masses *.

The method of entry of the parasites may be studied by examining the outside of the coral, and then making thin sections, both transverse and longitudinal and radial and perpendicular to the surface. In doing this the nature of the minute thread-like green filaments in and on the coral should be noted, and some specimens should be decalcified with them attached. Perfect septa of recent corals, which have not become dry or which have been lately soaked, may often be examined satisfactorily without sections being made, and the network of ramifying tubes may be readily observed in them; for a coral structure well permeated by its natural medium is much more transparent than the dry section which may be made from it.

The sections of the hard structures may be examined after being placed on slides (a small quantity of Canada balsam being used to cause them to adhere) without any covering; and the decalcified specimens, after being washed in water, may be mounted in cells with glycerine.

Reflected light may be used satisfactorily with a low magnifying-power in examining the dry section; for it exhibits the remarkable silvery appearance of the bundles of minute filaments as they enter the theca of the coral, each filament being tubular and refractive.

A magnifying-power of 400 diameters and an achromatic condenser are the most useful appliances in examining transparent specimens and the decalcified structures by transmitted light; and the ability to see the long tubes of very different calibres perfectly and well-defined, and distinguishable from the spicula and their intermediate dark edges, is only possible under a well-corrected object-glass.

The following order of examination should be followed:—(1) The examination of the canals on the inside and in the septa of corals; (2) the examination of corresponding decalcified specimens; (3) the examination of the outer structures, so as to determine the mode of entry of the parasites, hard and decalcified specimens being used; (4) observations should be made in and about those parts of corals where there is much organic basis amidst the sclerenchyma and between the two laminæ of a septum, and the large size of the associated filaments noticed in solid and decalcified specimens.

IV. *The usual appearances of Typical Parasitic Canals.*

On examining a thin dry section of a coral, made at a little distance from the outside, or on looking through a transparent septum, the para-

* The process of carbonization in these delicate filaments and spores may be imitated very significantly by placing some of them under the influence of slight heat and pressure. A thin glass cover being put over a mass, and a spirit-lamp flame being held beneath, it will be found that blackening of some of the vegetable structures will ensue, without the application of much or continuous heat.

sitic borings, when present, usually resemble long dark lines with a longitudinal and central transparent space. The lines may branch here and there, and usually at a considerable angle, and they often dip out of and come within the focus of the microscope in their more or less long course. They are singularly persistent as regards their calibre, which, always small, is unchanged even in the branches and branchlets. The commonest tubes (for such are these linear and longitudinally luminous appearances) are about from $\frac{1}{5000}$ to $\frac{1}{8000}$ inch in diameter. They are simple excavations, tubular in shape, and they have no special hard tubular wall. Each contains a vegetable filament, consisting of a tubular cell-wall and contents. They are cylindrical, and the breadth of the longitudinal light line depends upon the amount of vegetable material within the tube, upon the shape of the perforation, and the nature of the surrounding hard structures. When the cytioplasm of the filament which is within the continuous cell-wall is simply glairy matter, the tubes are often difficult to distinguish, as their whole lumen is transparent; but when the tubular cell-wall is crowded with granules, the light does not pass at all, and the whole tube appears as a dark line. Between these conditions are many, and which refer to the amounts of granular cytioplasm here and there in the same tube. The aggregation of granules determines the clearness of the longitudinal light line, its loss here and there and its replacement by a kind of moniliform appearance of alternate light and shade (Plate 6. figs. 11–17).

The parasitic canals, although they often branch out and ramify widely, rarely inosculate with others.

Another very common kind of canal is seen in the same situations, and also throughout the whole coral; it rarely pursues a straight course, but bends and curves first on one side and then on the other, and branches, either perfect or stunted, come off from the convexity of the curves, usually directly tangential to them. The stunted branches are short and linear, and give a very marked appearance to the canals, especially when they terminate in a spherical end with or without a branch from it. One of the numerous appearances is that of a straight canal bifurcating at right angles, and the continuation of the original canal assuming the form of a short stunted end just beyond the branching. Sometimes this abrupt termination is enlarged and, moreover, less globular in shape (Plate 6. figs. 16–19).

Swellings or enlargements of the calibre of the canals are not infrequent, and they are usually impervious to light. It will be noticed in most specimens of long canals that there is a peculiar wavy outline of their path, the excavations not being absolutely in a right line but in a series of minute and continuous curves.

In some specimens the canals are very long; in others they are short, and every variety may be seen in the same section. The direction which they take, and often their length, depend upon the minute structure of the hard parts of the coral.

The number of the canals varies also in different specimens, age and bathymetrical range regulating the parasitic growth more or less; they are more common in the corals with lax textures like the *Perforata* than in the *Aporosa*.

In some of the inner parts of the hard deep-sea corals the canals are few in number and are very long and narrow. These interior canals often give off, either from their whole surface, from parts of it, or only from the swollen parts, long and very delicate tubes of from $\frac{1}{10,000}$ to $\frac{1}{20,000}$ inch in diameter; but this appearance, which is very common in such species as *Balanophyllia verrucaria* and *Caryophyllia clavus*, var. *borealis*, is extremely rare in others (Plate 6. figs. 20–28).

When parts of corals corresponding to these interior sections and septa are decalcified, a repetition of the appearances of the canals is seen in the arrangement of their contents. Each canal contains and has its interior lined by a homogeneous transparent tubular cell-wall, and this contains fluid and more or less solid contents here and there.

The cell-wall is continuous through all the ramifications, and ends abruptly in the stunted branches, and it lines the globular ends and all the swellings. It can be traced to give off the extremely delicate tubules to the minutest ramifications just noticed. The cell-wall structure appears to lie against the sclerenchyma of the coral, but not in a perfectly smooth canal; for there are minute pits and roughnesses on the inside of the canal, into which the tube itself does not fit (Plate 5. fig. 7, and Plate 7. figs. 56 & 57).

Cross partitions in these tubular cells are very rarely seen; and even in the majority of instances in which one might feel disposed to admit their occurrence, it is possible that the dissepiments are more apparent than real, being the result of light passing up between two closely approximated masses of granules (Plate 7. figs. 58–60).

This coalescing of granules in masses, with spaces between them, is commonly seen; and a moniliform appearance is also given to some minute tubes by a corresponding arrangement of the cytioplasm (figs. 36 & 40).

No starch can be detected with the usual tests; but in many filaments there is evidently a bright sap-green tint, which is increased when light is transmitted through the refractive cytioplasm.

Throughout, the resemblance of the canals and their filaments to a mycelium is very striking.

Occasionally a long and wide canal, crammed with granular cytioplasm, passes far into the substance of the coral and may be seen with those just described. It can be traced outwards to the surface of the coral, whence all the others come—some entering from without directly, and others being branches of canals situated close to the outside or offshoots of what appear to be cavities filled with oospores (Plate 5. figs. 2–5).

V. *The Parasitic Canals near the exterior and their Methods of entry: Reproductive Elements.*

The finer canals and those of all diameters except the very smallest may be occasionally traced to the outside of the hard coral-structure, so that the method of entry of the parasite can be determined. This is greatly assisted by decalcifying, after noting the character of the vegetation, which is inseparable, except by tearing, from the wall of the specimen.

Methods of entry.—1. Rarely a long typical canal may be seen opening out through the coral-wall without any increase of calibre.

2. Dark globular or short cylindrical-shaped cavities exist in the very outside of the theca, and usually in such positions where the external ornamentation or where the intercostal spaces admit of substances resting readily. The cavities are large, and vary from $\frac{1}{500}$ to $\frac{1}{1000}$ inch in diameter; their contents give a dark and opaque appearance to them, and they give off many very fine short canals, canals of larger calibre which pass more or less inwards, and the common long ramifying and non-inosculating canals, there being one or many of these (Plate 5. figs. 1–7 & 10).

3. Long, straight, and also curved canals of large calibre, $\frac{1}{500}$ to $\frac{1}{1000}$ inch, usually constricted here and there, and in some instances having hemispherical projections. They sometimes pass far inwards (Plate 5. fig. 8), and then their contents are usually not so crowded as to prevent light being transmitted; and, indeed, in one specimen long portions of the canal were deficient in granular, and were filled with homogeneous and clear cytioplasm. Sometimes the wide canal ends in a *cul-de-sac*; but in most instances smaller canals pass off irregularly from it, and even some of the minutest.

4. Irregular excavations occur on the surface of the coral of no great depth, into which shallow cup-shaped depressions enter; and these are either with sharp edges and give entry to a typical tube or to many fine and short tubes in addition (fig. 10).

There is in a specimen of *Flabellum laciniatum* a tunnel reaching inwards from one of these irregular excavations which has three more or less globular enlargements on it, the last being continuous with a very short prolongation of the tube.

5. Great numbers of very branching canals form a close network and extend into the coral-structure, usually from the top of a costal or septal ornament, in *Balanophyllia verrucaria* for instance. These glomeruli arise from a depression in the outside of the coral, or from a decided large penetration, and it appears as if a mass of oospores had collected therein and germinated (Plate 5. fig. 1).

Transverse sections, of necessity, cut through these masses of branching and anastomosing tubes at different angles; and it is possible, therefore, by comparing numbers from the same coral to estimate the length of a mass and to recognize the typical canals which eventually arise from it.

Longitudinal sections made parallel with the septal ends often exhibit these glomeruli to perfection; and under a low power they may be seen as bright refractive tube-masses entering the coral at stated intervals. This appearance is also presented in old corals in transverse sections (fig. 29).

Observations on Decalcified Specimens of the Outer Parts.—After submitting sections or pieces of corals known to present the appearances just enumerated and described to dilute hydrochloric acid until the hard parts are destroyed and the organic basis-structure remains free, they should be washed in distilled water; and portions of the remaining matter may be put up in thin cells with glycerine slightly diluted.

The organic tissue is usually preserved in films, but occasionally, and especially in the semiperforate *Balanophylliæ*, masses of it may be obtained conforming to the widely reticulate structure of the exterior of the coral. It is transparent, almost homogeneous, and only granular here and there; but the paths of many fine parasitic filaments may be traced in it. Usually the occurrence of larger canals determines the raggedness and breaking-up of the organic film as a whole, as they have drilled through and along it in all directions.

Surrounding this tissue, and usually inseparable from it, are the vegetable parasites, now freed from their calcareous covering.

Reproductive Elements.—Oospores, zoospores (non-ciliated), separate or in masses, and the latter often within filaments, large confervoid-looking filaments, large unicellular tubules crowded with dark cytioplasm, and filaments of different lengths and diameters and with numerous or few branches (all bearing a definite relation in point of size to the canals whence they came) are readily seen and distinguished.

The extremely fine canals, $\frac{1}{10,000}$ inch, do not usually yield any filaments after decalcifying has been even very carefully done; but I have been able to draw a few, which are all the more interesting because they are evidently extremely delicate utricles arising from the fusiform or roundish zoospores which in this parasite, as in *Saprolegniæ*, germinate before expulsion and before having reached their true zoospore or mobile condition. In Plate 7. fig. 55, zoospores are seen with filaments, and in fig. 61 separate spores are delineated.

It is evident, after the examination of these filaments and their associated zoospores, that the cause of the furry appearance of some larger canals (Plate 6. figs. 21, 22, 23) is due to the development of corresponding growths from germinating cells within and their penetration of the hard parts after having perforated the parent cell-wall and the dense structure surrounding.

Rarely a minute tube may be seen passing off at right angles from one of the largest kind; they are usually short, and do not appear to come from within, but to be offshoots of the parent cell-wall.

Oospores are to be found closely adherent to the organic basis-structure and amidst the branching thread-like tubes which are inseparably attached

to the outside of the corals. They are also to be distinguished in fossils, crowding the cavities on the outside of the coral and some of the dissepimental spaces; but I have failed to see them in corresponding numbers and positions in recent forms.

The oospores are large, and reach $\frac{1}{1000}$ inch in diameter. They are usually globular, but sometimes slightly lobular; and in the latter case there is an evident internal grouping of granules which makes the mass look like a tetraspore. They are dark in colour, and there is an external cell-wall. Becoming fixed to the coral-wall, they sometimes flatten out and remain as circular black spots, a long filament being continuous with them and passing into the hard structure; but as yet I have not seen a satisfactory tubular prolongation of a globular spore, except in the Silurian *Goniophyllum*, where they present beautiful tubes.

VI. *The large confervoid-looking Filaments within the Organic Basis.*

The septa of all Corals are in two longitudinal parts, which are separated more or less perfectly in the median line. Hence transverse sections show in the septa of recent corals two cut surfaces, each representing the top of a plate or lamina separated by a linear space or by a corresponding organic tissue. In some species this intermediate structure reaches the surface at either the calicular or the costal edge of the septum. It is the relic of an involution of the dermal structures in and around which the sclerenchyma was deposited. Moreover the organic structure thus intermediate really passes into the septal laminæ in all directions, as can be proved by decalcifying them. It would appear that the younger the coral is, the more distinct are these intermediate structures, and that with age they become more or less filled up with carbonate of lime, and may finally thus become obliterated. Certain genera of rapidly growing forms appear to have the spaces more distinctly developed than others.

These organic structures, coming to the surface of the coral, of course are, under favourable circumstances, soon attacked by penetrating parasites; and the possibility of entry and of growth is so great in some instances, that wide layers of very confervoid-looking growths flourish, and present a very peculiar appearance under the microscope (Plate 7. figs. 33–35). The filaments forming one or more layers are nearly parallel, are large (from $\frac{1}{1000}$ to $\frac{1}{2000}$ inch), rarely branched, and exhibit transverse markings, which are not true articulations, although the filament frequently breaks off at them. The filaments are tubular, and have a distinct cell-wall, which is swollen out here and there; and their cytioplasm is aggregated more or less regularly, and in some places resembles conidia. Little processes project from the wall of the filament here and there, and are of about half the calibre of the parent tube. In some filaments the cytioplasm is well separated from the wall, but usually it fills the whole tube.

The jointed or articulate appearance is particularly visible when the fila-

ments are only in the organic substance or are only surrounded by very thin films of carbonate of lime; for when these large tubes penetrate the solid parts of the septa their diameter appears to be slightly less, their cell-wall ceases to be distinguishable, and their contents are usually undivided. But occasionally it appears that some burrow very successfully, and a long and wide tube results, which, in the majority of instances, is full of granular cytioplasm and rarely sufficiently empty to exhibit a central bright band of transmitted light.

The Minute Filaments from the large kinds.—Although the broad filaments found within the septa (especially of *Caryophyllia clavus*, var. *borealis*, of *Flabellum laciniatum*, Edw. & H., and of *Balanophyllia verrucaria*) do not often bifurcate or ramify, yet they now and then give off long ramifying but not often anastomosing filaments of extreme tenuity. They are found in crowds in some spots of the septa, and their diameter is about $\frac{1}{20,000}$ inch, their general distribution and method of branching being a very exact counterpart of some of the larger growths already noticed as occurring so frequently in the other hard structures of corals.

Usually these very fine canals retain the same diameter throughout their length. In some corals they do not run a long course, but bend soon or even ramify abruptly, and in both cases pass into irregularly shaped cavities, emerging from them at the opposite end or absolutely terminating in them. These cavities are not unlike ill-developed bone-lacunæ in appearance, and are frequently found in series on the periphery of masses of long, radiating, spicular structures. Usually of very small size, and more or less irregular in shape or elongate, they sometimes are the cut ends or tubes of irregularly shaped parasitic borings which have been formed by another and larger filament.

The resemblance of these fine canals to those which pass off so frequently from the larger parasitic tubules in the thick wall or columella of the same or other species of coral is very exact, and probably they have the same cause of origin.

Large confervoid-looking Filaments in the Body of Corals.—In transverse sections of some corals, especially in the genera *Lophohelia* and *Solenosmilia*, some long rows of the very large confervoid-looking filaments are often seen cut across more or less obliquely. These rows are formed of numbers of large tubes placed side by side and in one or more layers, and they occur in those situations where involutions of the dermal structures took place during the growth of the coral. These tubes give out fine ramifying tubes such as those just mentioned, and which usually terminate in irregular-shaped cavities.

But usually the contents of the large tubes are crowded and not separated off, and it is rare to see spaces in them through which light can penetrate. They branch, and usually produce ramifications which are of the same diameter as the parent filament; and where they are cut across they present an irregular granular appearance, which is partly due to

the cytioplasm and partly to the existence in the canal-wall of minute more or less perfect perforations. It is evident that the canals of these large parasitic filaments may be correctly compared with the larger long and short penetrations on the outside of the corals, which are the means of entry of the bulk of the parasitic growths.

VII. *Method of Entry and Growth of the Parasite.*

It is evident from the examination of the sections of the outside of corals that the parasite obtains entry below the living dermoid tissues of the coral at spots where there is usually a crowd of competitors for attachment, shelter, and also for boring. Some minute cavities on the outside, either the result of the operations of other organisms or the product of the ornamentation of the coral, evidently and constantly contain masses like large conidia or oospores or shapeless masses of granules. The boundaries of these cavities often relate to the intermediate spaces between columns of spicula peculiar to the coral sclerenchyma; the organic basis of the hard structures comes in abundance close to the outside of the theca in such positions, and it is the particular food of the mycelium about to enter. The tubule of the ingrowing parasite comes from a conidium, oospore, or from a granular mass which probably is a zoospore; and the entry can only be by growth-force, and by the assimilation and removal of the organic basis, together with the dissolution of the carbonate of lime of the coral by the development of carbonic acid from the end of the tubule. The existence of movement in the cytioplasm and possibly in the cell-wall may be reasonably inferred; and this would tend to drive out fluid between the hard walls and the soft internal tube. The solution appears, however, to be only active at the growing end of the tubule; and this growth is clearly often stopped by a hard and solid mass of spicula, there being an insufficient quantity of the organic film there for the nutrition and *vis viva* of the parasite. It is evident that the entry must be made during the life of the corallite or very shortly after death.

There is one manner in which the parasite reaches the outside of the coral and becomes fixed so as to penetrate, which is very remarkable and also suggestive of the group of Thallophytes to which it belongs.

Species of *Bryopsis* and *Cladophora* were living in the aquarium with the *Balanophylliæ* which were afterwards cut and, in some instances, decalcified. These reticulate and dark green forms grew upon the lower parts of the corals, where the bright orange animal matter was no longer existing; and, as the corals grew weak in their nutrition and the tentacles rarely expanded, there was an evident struggle between the vigorous plants and the dying Cœlenterate. At last extremely fine filaments of *Bryopsis* appeared on the septa, and, as the thin films of living tissue grew smaller, they encroached more and more.

I thought at first that the penetrating parasite was either a "rootlet"

of *Bryopsis* living under extraordinary circumstances, or that it was a modified form of it, especially as I noted instances where the filaments of this plant had penetrated and perforated through projecting nodules and ridges of the hard parts of the coral.

The adhesion of the *Bryopsis* would give the delicate filament about to penetrate a *point d'appui.* But on placing some tubes of *Bryopsis* which had short filaments on their outsides, like those obtained by decalcifying, in glycerine, this liquid speedily entered what appeared to be the tubular structure of the plant, filled with dark green granules and cytioplasm. It filled the tube and made the cell-wall sufficiently transparent to show that there were no cell-contents, but numerous filaments of an Achlyan-looking parasite. These had penetrated the *Bryopsis*, had grown at the expense of its cytioplasm, and, finally, they were making their way out through the wall and coming in contact with the coral.

I have not been able to trace the mobile zoospores of the Achlyan or the origin of parasitic filaments from them; but it is evident that the parasite exists on the outside as well as within the coral, and in the tubular or vegetative form, and that the external filaments contain immature zoospores which develop tubules which penetrate the parent wall, impinge against the coral, and penetrate (Plate 7. fig. 55).

VIII. *Structure of Reproductive Elements and Classificatory Position.*

The parasites, whether enclosed within their tubular perforations, which assimilate to their shape, or rendered visible by the action of dilute acid, or when free on the outside of the corals, present the appearance of the mycelium of fungi of such orders as the Hyphomycetes and Physomycetes. The filaments, whatever may be their diameter, are furnished with a continuous cell-wall, and dissepiments are extremely rare, being only recognized once or twice in hundreds of specimens. The filaments rarely inosculate, but branch either rarely or with great frequency. There are often secondary and other branchlets; and the width of the calibre of the whole tube is usually maintained.

It is very usual for branching to take place at right angles to the parent filament, and for a small rounded continuation of the last to form beyond the ramification.

More or less globular or hemispherical swellings occur on the side of the filament, and occasionally it is swollen out into one or a succession of spherical enlargements. The filaments terminate in *culs-de-sac* usually of the same diameter as the rest of the tube; but globular or irregular-shaped enlargements are by no means uncommon at their ends. In all this the parasite resembles many fungi. It is towards the ends of some smaller filaments that a cell-dissepiment occurs, separating a terminal portion, only filled with dark cytioplasm, from the rest of the filament, which often contains a refractive fluid with large granules here and there (Plate 7. figs. 49–61).

The cell-contents of the filaments are:—

1. Glairy transparent fluid; this renders the canals often difficult of distinction, and staining with carmine renders them usually visible.

When removed from their canals the filaments, without any other cell-contents than this glairy matter, usually show a very distinct cell-wall with occasional refractive granules close to it in a few places. Usually there is no colour present, but in some specimens the glairy fluid is tinted a faint yet bright sap-green.

2. Dark-coloured, brown or black, cytioplasm collects here and there in the filaments, with interspaces where the clear fluid mentioned above is present; or the whole tube may be crammed with the structureless and dark mass. This cytioplasm often aggregates in regular and consecutive portions of the tube, and the intervening colourless fluid gives the appearance of cell-dissepiments.

In most tubes the dark cytioplasm, small in amount, is situated close to the cell-wall, and, there being some structureless clear fluid in the axis, the filaments are refractive.

Granules, excessively minute, form in the coloured cytioplasm, and conidia gradually develop here and there by their aggregation in all parts of the filaments. Small ovoid bodies with two or three minute dark molecules within them, besides a refractive fluid, are formed out of this cytioplasm within the filaments, and in the enlargements, and on them, and at their ends.

No special terminal cell containing these reproductive conidia and sporidia (zoospores imperfectly developed) appears to exist; but probably the rounded and elongated ends of some filaments are the analogues of the terminal fructification-cells of their congeners.

The passage of extremely minute tubes from larger filaments, through whose walls they penetrate, and the presence of small ovoid bodies giving out minute filaments within the parent cell-tube, are very suggestive phenomena. They coincide remarkably with some parts of the life-cycle of the *Saprolegniæ**; and this resemblance is enhanced by the presence in the coral parasites of the terminal filaments cut off by a cell-diaphragm from the rest. Moreover the globular endings to many of the filaments, or the spherical offshoots of many, greatly resemble some of the parts of species of *Saprolegniæ*†. But whether a cell-wall cuts off the globular cell in the coral parasite, I have not been able to determine; and all the evidence I have is against this being the case.

Outside the coral are long, branching, inosculating filaments, very rarely divided by partitions, and crammed here and there with zoospores, which often produce filaments when still within the cell-wall. Finally the oospores are large, spherical, and apparently arise from compound masses or oogonia. All these details connect the parasite with the

* Thuret, Ann. des Sci. Nat. t. xiv. pl. 22. fig. 8.

† Thuret, *op. cit.* figs. 10, 11.

Saprolegniæ; but a specific identity with *S. ferax*, Ktz., is wanting. As in another work I have absorbed *Saprolegnia* in *Achlya**, I propose to classify this parasite in that genus, and to name it *Achlya penetrans*.

But in thus provisionally classifying these parasites, their resemblance to the filamentous rootlets of *Codium* and to very delicate specimens of *Bryopsis* must not be forgotten. The large confervoid-looking filaments found within the interlaminar structure of the septa closely resemble those of the *Bryopses* which cling in a close reticulation to the outside of many corals. *Bryopsis*-filaments do penetrate projecting parts of the coral. The tint of the clear cytioplasm of the parasite is often pale sap-green; but there is no other evidence of the existence of chlorophyl in the contents of any of its very variously shaped filaments. The *Bryopsis* is, of course, crowded with green granules, and doubtless chlorophyl is present. The reticulate rootlets of *Codium* are often colourless, the larger and upright portions of the plant being green. The probability of the presence of chlorophyl being determined by the action of light upon colourless or dark brown cytioplasm should therefore be considered before an arbitrary line is drawn between the *Achlyæ* and such very remarkable forms as those included in the genera mentioned above.

From the results of my examination of Upper-Silurian corals and of Lower-Silurian arenaceous Foraminifera, it is evident that a parasite closely resembling *Achlya penetrans* lived within them during those remote ages. Corresponding in shape with the Silurian form of parasite are others which are fossil within the corals of later ages. The main differences between the ancient and the modern forms consist in the larger calibre of some of the filaments of the first, their long, often unbranching course, and the frequent development of *Conidia*-looking bodies within them, and the spherical shape of the spores; but it is quite possible that these are not distinctions which are of a specific value.

The modern coral-parasite is evidently the descendant, with slight or, possibly, no modification, of those which flourished during successive world-wide changes in floras and external conditions. Hence it would, in all probability, have had its life-cycle made complicated, and a metamorphosis involving vegetative and mobile stages has been superadded. It is not an assimilator of putrescent or rotten animal matter, but of the nitrogenous and undecomposed organic basis of the coral; and in this it resembles the organisms which destroy some living Diptera and other aërial insecta. Moreover this resemblance in function is possibly caused by continuance of individuality; and if this be true, it adds vastly to the difficulty of placing the parasite in a philosophical scheme of classification. *Empusina* (the fly-killer) certainly is an aërial form of *Achlya*; and *Empusina muscæ* turns into *Achlya prolifera*. It is, then, quite within the range of possibility, and, indeed, it is extremely probable, that the

* Micrographic Dictionary, 1875, 3rd edit., Articles *Achlya* and *Saprolegnia*. See also *Sporendonema* and *Empusina*, and Article on Confervoideæ.

coral *Achlya* is the aquatic form of some aërial "fungus" which, like it, devours and increases upon organic matter.

Some of the most perfectly developed *Achlyæ* parasitic within corals were obtained from specimens of *Balanophyllia verrucaria* which came from the Mediterranean, and which I kept for many months in an aquarium. The vegetation in the aquarium consisted of species of *Cladophora* and *Bryopsis*, and they grew not only on the rockwork, but also on the bases and sides of the corals which had been left uncovered during growth by the orange-coloured ectoderm. As some of the corals became weak, their colours becoming pale, the organic or living tissue being thinner and the tentacles less expanded, the weed encroached and, finally, in one or two instances appeared on the septa, the living ectoderm having become abraded or dead on those spots.

After a while a bulky "mould" spread over the whole calice of the coral, and decomposition soon set in. This mould consisted of extremely crowded filaments with occasional dissepiments, and resembled a *Botrytis*. It lived in the water, and grew with great rapidity.

This fact renders Berkeley's statement that *Achlya* may be an aquatic form of *Botrytis* very probable; and certainly the filaments of many of the internal parasites of the corals greatly resemble those of *Peronospora*. If, then, the coral-parasite follows the life-cycle of its congeners, it may live under different conditions in various organisms, and receive as many generic titles and specific names.

Doubtless there is a motile stage as a freely swimming zoospore in one of the life-cycles; and in this this feeder on organic matter relates to its remote ancestry amongst the Amœboids.

If the arbitrary nature of all the classifications of organisms which assume different shapes and habits under different external conditions be admitted, the position I have assigned to the parasite as *Achlya penetrans* appears to be correct. But it may be more philosophical to state that it belongs to a group of interchangeable forms, and that it is the marine and parasitic expression of the arbitrarily separated genera *Achlya*, *Saprolegnia*, *Botrytis*, *Peronospora*, and probably *Bryopsis*.

IX. *On the Occurrence of* Achlya (Saprolegnia) ferax, *Ktz.*, *in* Caryophyllia Smithi.

On submitting an old specimen of the common broad-based *Caryophyllia Smithi*, from the Devonshire coast, to the action of dilute hydrochloric acid, a vast amount of internal parasitic growth was obtained. This growth in some respects resembles that of *Achlya penetrans*; but in its close reticulations of long and rarely branching filaments, of $\frac{1}{8000}$ to $\frac{1}{10,000}$ inch in diameter, it assimilates to the well-known parasites of *Anomia* and *Ostrea*.

The resemblance of the fructification to the drawings in Kützing's

'Physiologia Generalis' of *Saprolegnia ferax* is very close (Plate 7. figs. 36, 37, 38, 40, 41).

There is an interesting point about this Achlyan from the English littoral zone, and that is its resemblance in tint to those of the deeper sea. The delicate sap-green of the homogeneous viscid granuleless refractive cytioplasm is evident enough. Many filaments, however, are colourless.

X. *Summary.*

Quekett, Rose, Wedl, Kölliker, and Moseley have noticed and described the borings of vegetable parasites in molluscan shells, fish-scales, and corals; but no special attention has been paid to the filaments penetrating the last-mentioned organisms.

Corals from the littoral zone down to 1095 fathoms are frequently the seat of the parasitic growth of two kinds of *Achlyæ*, whose horizontal range is from Davis Straits to the tropics and 15° S. lat.

Fossil corals of Silurian age were also affected by closely allied, if not specifically identical, growths.

The method of investigation is by making thin sections of the sclerenchyma, and also by dissolving out the carbonate of lime.

The parasites are filamentous, and fill up the canals which they form; they resemble a mycelium, and penetrate the coral, living upon the organic basis, and having their length, breadth, and straightness, or branchings, dependent on the peculiar nature of the arrangement of the spicula in the different species of the Madreporaria. The entry is made from oospores, zoospores, and by the accidental contact of the parasites whilst perforating algæ situated on the wall of the coral; and the penetration and growth appear to be the combined results of the formation of a soluble bicarbonate of lime by the action of carbonic-acid gas evolved from the growing end of the tubular filament, of the pressure incident to growth, and of the movements of the cytioplasm and the cell-wall.

The vegetative life of the parasites is accompanied by reproductive efforts within the corallite; for the aggregation of granules within the viscid transparent cytioplasm can be detected, and their formation into large conidia and into small unciliated zoospores also.

Following the peculiar physiological habit of the Saprolegnian group of *Achlyæ*, the reproductive elements germinate and produce either large or very small tubes which, after penetrating the parent cell-wall, get through the solid investment, and become indistinguishable from the filaments derived from spores attached to the outside.

The diameter of the largest canals containing filaments in which there is occasionally a doubtful dissepiment, and which flourish in the organic matter between the laminæ of a septum, is $\frac{1}{500}$ inch; that of the typical and ordinary tubes is from $\frac{1}{1500}$ to $\frac{1}{8000}$ inch; and the finest tubes are as small as $\frac{1}{20,000}$ inch in diameter.

The canals and included filaments in some instances increase in calibre at certain spots, and even form globular expansions, but usually the same diameter is retained; the enlarged portions relate to the reproductive process. The cell-wall of the filament is in close contact with the sclerenchyma of its canal.

In a littoral species (*Caryophyllia Smithi*) the parasite is identical with *Saprolegnia ferax*, Ktz.; but there is a manifest distinction between it and those of the other forms. The parasite of the littoral coral greatly resembles those of the shells of Mollusca and of the scales of fish. Although it is quite possible that all the parasites of the corals described may be referred to one species, their type being altered by the peculiar conditions surrounding them, still it is thought advisable to regard them as members of two species. The classificatory position of the parasites is in the midst of a group of forms which have complicated life-cycles, such as the Achlyans (proper), the *Saprolegniæ*, and *Empusinæ* and Botritidæ, and the filamentous false-root bearing genera *Codium* and *Bryopsis*—forms which are more or less the expressions of one organism under different conditions and age.

EXPLANATION OF THE PLATES.

Plate 5.

Fig. 1. *Balanophyllia verrucaria.* A longitudinal section of the coral close to the end of a septum, showing masses of the tubules of *Achlya penetrans* close to their entry. × 40 diameters.

Fig. 2. *Caryophyllia clavus*, var. *borealis.* A large tubular excavation opening out at the surface of the coral. × 350 diameters.

Fig. 3. Another excavation.

Fig. 4. A large tubular excavation cut across and exhibiting tubes of the parasite coming from it. × 350 diameters. The same coral as figs. 2 & 3.

Fig. 5. A transverse section of a tube found in the midst of the same coral; it shows the porose condition of the tube-wall and some branches. The coral-structure around is not shown. × 350 diameters.

Fig. 6. The origin of a long parasitic tubule from a large entry-tube. × 350 diameters.

Fig. 7. The porose condition of the wall of the tubular cavity, and very minute tubules coming off from the perforation, and a long and larger tube are shown. × 350 diameters.

Fig. 8. A series of dilatations in a large entry-tube. × 300 diameters.

Fig. 9. A large tube branching. × 300 diameters.

Fig. 10. A partly normal and partly parasitically formed concavity at the edge of a coral, with minute tubules and a larger tube coming from it and penetrating the coral-structure. × 300 diameters. All these views from fig. 2 inclusive are from the same coral.

Plate 6.

Fig. 11. *Flabellum laciniatum.* Typical parasitic tube of *Achlya penetrans* filled with cell-wall and cytioplasm.

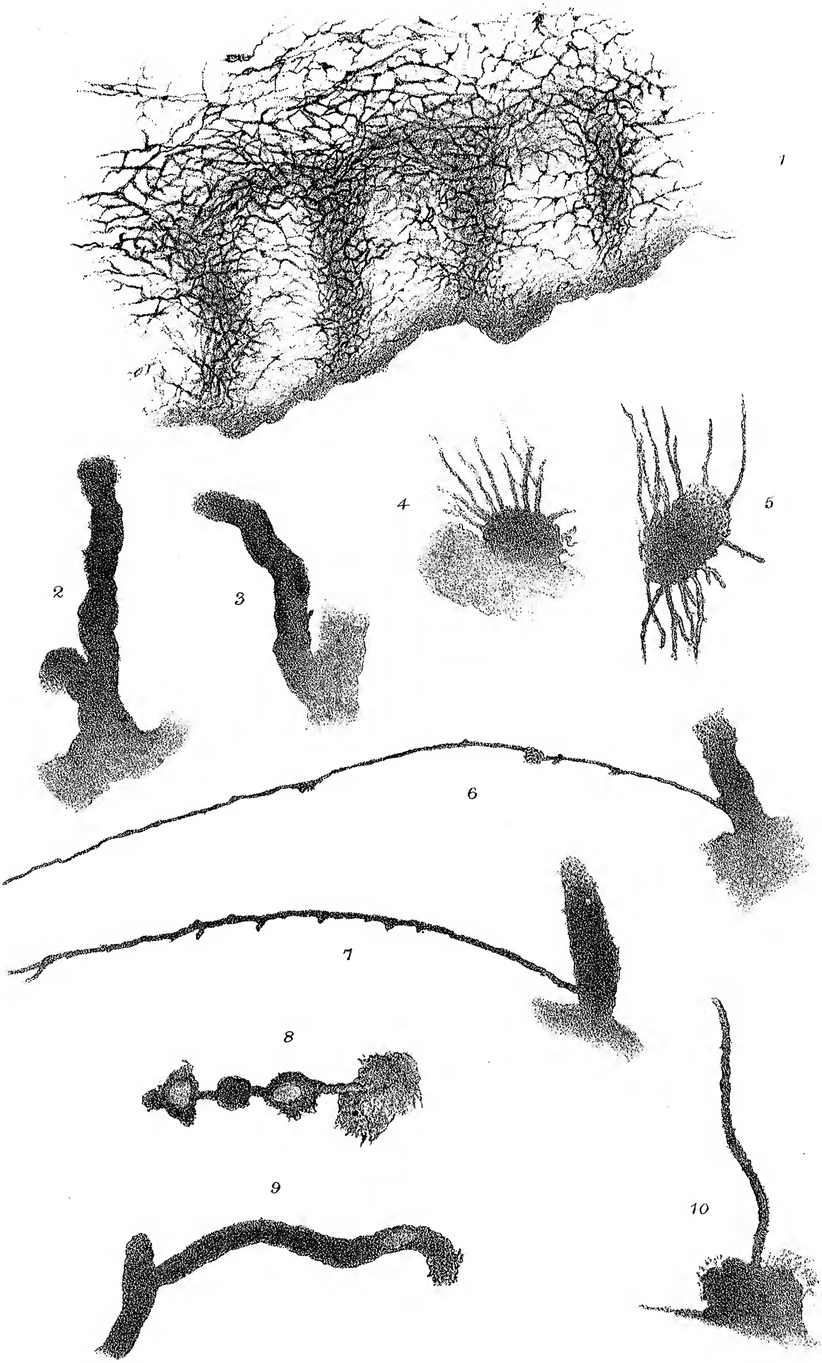
Figs. 12–15. Various shapes of typical tubes.

Figs. 16, 18, 19. Tubes branching at right angles and terminating in a blunt or globular head.

Fig. 17. A ramose tube. These drawings (figs. 11–19) are from one coral, and are magnified 300 diameters.
Fig. 20. *Balanophyllia verrucaria.* A parasitic tube showing minute furry-looking collections of lateral branches. × 350 diameters.
Fig. 21. Same subject. The tube entering and branching.
Fig. 22. Glomerulus and ragged tube. × 350 diameters.
Fig. 23. A parasitic tube entering, having glomeruli and ending. × 350 diameters.
Fig. 24. Globular terminations. × 350 diameters.
Fig. 25. A tube with glomeruli. × 350 diameters.
Figs. 26, 27, 28. Long and very minute tubules coming from a typical tube and some conglomeruli. × 350 diameters.
Fig. 29. Entry of tubes. × 40 diameters.
Fig. 30. A tube ending in an enlargement with commencing offshoots. × 350 diameters.
Fig. 31. A globular termination. × 350 diameters.
Fig. 32. A termination with a tube springing from it. × 350 diameters. All the views from figs. 20 to 32 inclusive are from the same coral.

Plate 7.

Fig. 33. *Lophohelia prolifera.* Large tubes nearly filled with cell-wall and cytioplasm within the interlaminar space of a septum; minute tubules come off, and occasionally end in spaces or lacunæ. × 350 diameters.
Fig. 34. Minute tubules and lacunæ. × 350 diameters.
Fig. 35. Large interlaminar tubes. × 300 diameters.
Fig. 36. This and all the following figures are taken from decalcified specimens put up in glycerine. Some swelling of the parasitic supports occurs. A fine ending of a tube, showing wall of parasite (*Saprolegnia ferax*), unicellular and ovoid bodies with one or more granules in them. × 350 diameters. From *Caryophyllia clavis*, var. *Smithi.*
Fig. 37. A ramose filament of *Saprolegnia ferax*, very characteristic. The cytioplasm is colourless. × 400 diameters.
Fig. 38. Filamentous tubes with globose endings. × 400 diameters. Figs. 37 & 38 are from the same coral as fig. 36, and refer to *Saprolegnia ferax.*
Fig. 39. Filaments of *Achlya penetrans* from *Balanophyllia verrucaria.* A mass of them. × 350 diameters.
Fig. 40. A small filament of *Saprolegnia ferax* in *Caryophyllia clavis*, showing cell-wall and cytioplasm collected more or less in regular spots with vacant interspaces. × 350 diameters.
Fig. 41. A filament of *Saprolegnia ferax* with a dissepiment and ending in branches, and a globular mass filled with granules. × 350 diameters.
Fig. 42. A globular part of a filament with several refractive granules. × 400 diameters.
Fig. 43. A dissepiment in a filament of *Achlya penetrans* from *Balanophyllia verrucaria.* × 400 diameters.
Fig. 44. Filaments of *Achlya penetrans* from the same coral. × 400 diameters.
Figs. 45, 46, 47. Filaments of *Achlya penetrans* from the same coral. × 350 diameters.
Fig. 48. Oospore and filament of *Achlya penetrans* from surface of *Balanophyllia verrucaria.* × 300 diameters.
Fig. 49. Oospore.
Fig. 50. Moniliform appearance of cytioplasm in a filament from the same coral. × 300 diameters.
Fig. 51. A filament with a globular end and branches of *Achlya penetrans.* × 400 diameters.



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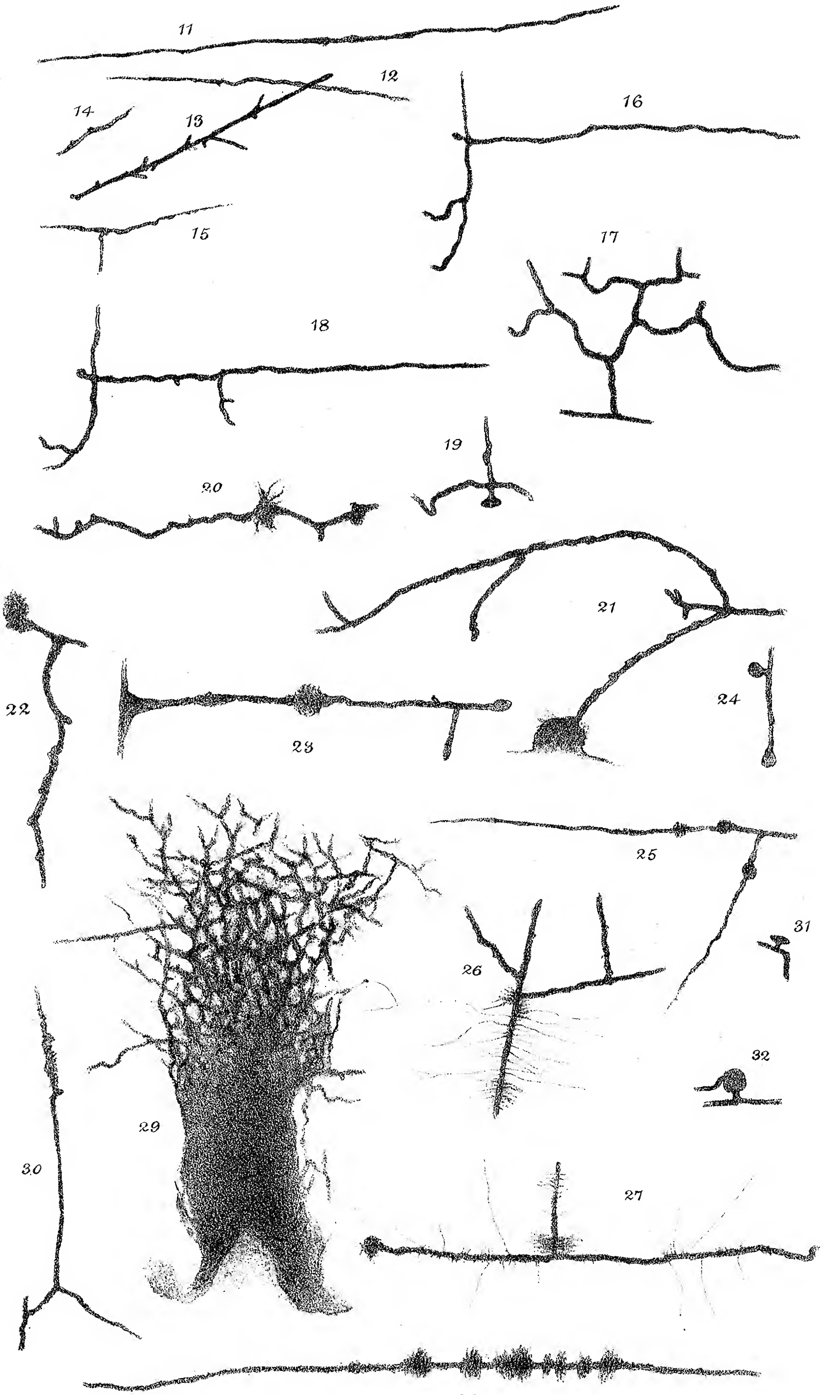

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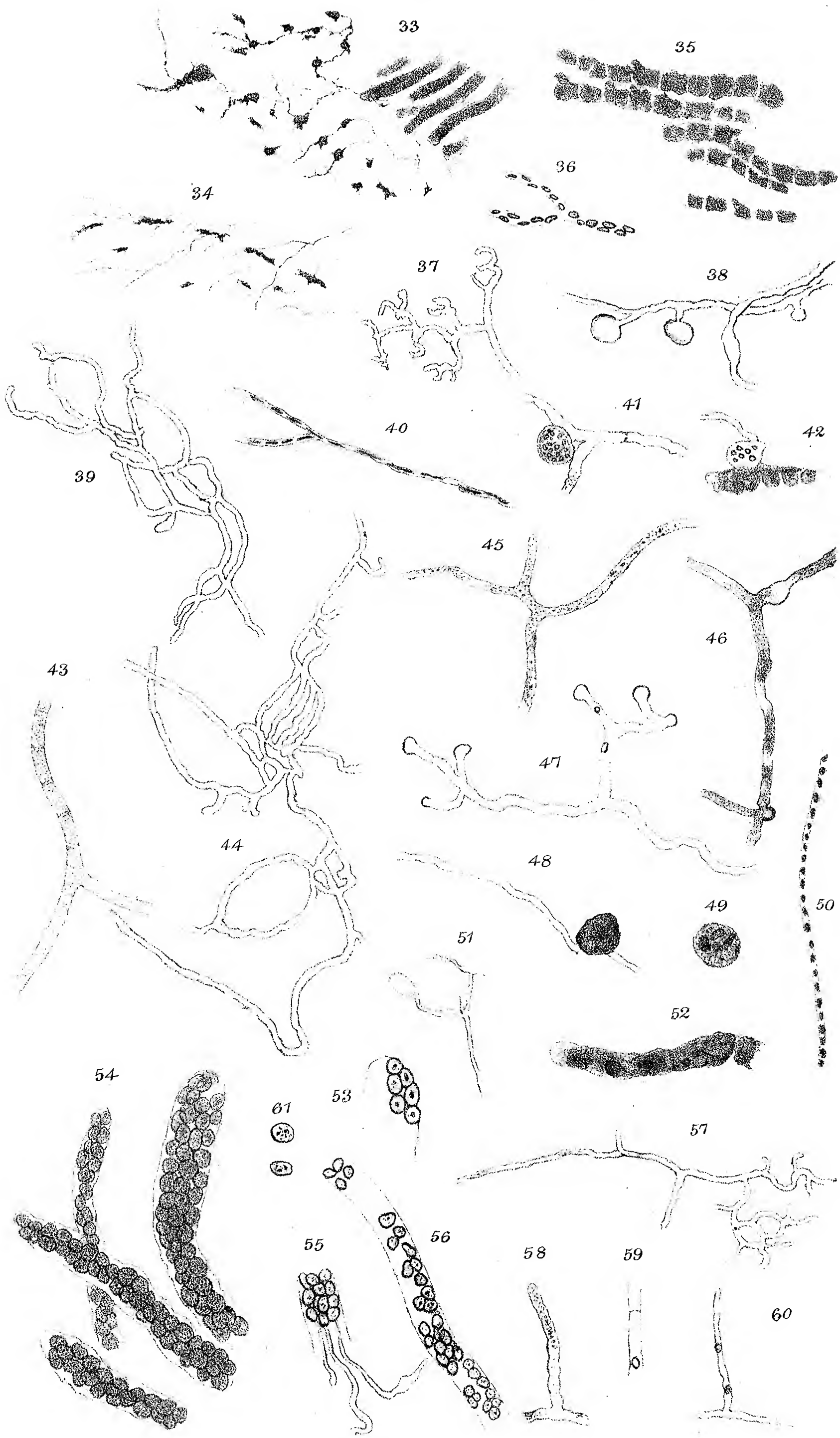

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Fig. 52. A large filament close to the entry of the *Achlya*, with conidia-like masses in the cytioplasm. × 400 diameters.

Fig. 53. A tubular filament ending and having numerous ovoid bodies close to the cell-wall (zoospores). × 600 diameters.

Fig. 54. Interlaminar tubes of *Achlya* crowded with cytioplasm. × 400 diameters. (See figs. 33–35.)

Fig. 55. Zoospores sending out filaments when within the parent filament. × 600 diameters.

Fig. 56. A filament like fig. 53.

Fig. 57. A typical filament of *Achlya penetrans*.

Figs. 58–60. Endings of filaments with dissepiments and granules. × 400 diameters.

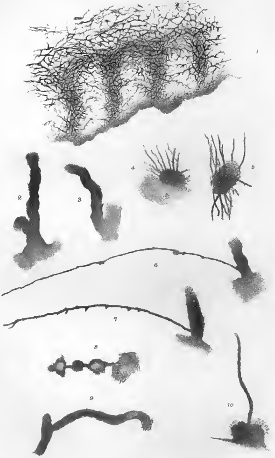
Fig. 61. Zoospores, non-ciliated. × 600 diameters (high eyepiece).

Appendix to a Communication on Thallophytes in Recent Corals. By Professor Duncan, F.R.S. &c. Received May 11, 1876.

Since my essay on the Thallophytes in Recent Corals has been sent to the Royal Society, I have become aware, after the examination of some deep-sea corals (depth 363 fathoms), that thread-like dark green organisms of a vegetable nature ramify on their surface and penetrate it. These filiform organisms are visible to the naked eye, and, when examined under the microscope, are shown to be unicellular and to contain green colouring-matter. They leave linear depressions on the surface of the coral which correspond with them in diameter and outline, and they penetrate and dip under the surface sometimes to reappear above. Their course may often be traced in *Amphihelia oculata* just below the surface without a high magnifying-power being used. From the stain which is often seen on the coral on either side of these superficial filamentous organisms, it would appear that they are sometimes broad; but the excavating filaments do not appear to have been broader than they were when they first penetrated or covered the corallum. I have traced the ramifications of these large filaments within the coral by dissolving in weak hydrochloric acid, and they resemble those described by me. They appear to be the same as those which are found in the interlamellar tissue of the septa, and the difference is only in size.

Having had the opportunity of examining some large Foraminifera from the Indian Ocean, I can testify to the presence in them of multitudes of small *Saprolegnia*-looking filaments, but which, like those described by Mr. Moseley, have green contents.

Finally, I have lately discovered that, besides the penetrating planta and spongida of corals, there are long tubular organisms which end in bag-like terminations so greatly resembling some of the calycles of Hydroida that they demand careful investigation. These filaments penetrate and also exist in the previous channels of *Cliona*.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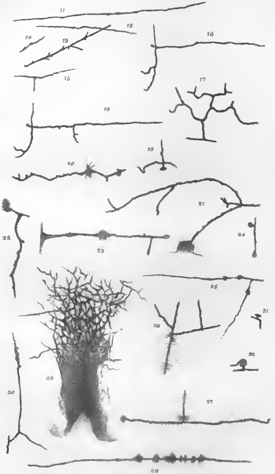
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